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Pleistocene Snakes of the Ozark Plateau

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Historically, zoogeographic studies of modern groups of amphibians and reptiles have been based on various interpretations of their present-day patterns of distribution (e.g., Cope, 1900, pp. 1199–1234; Darlington, 1948; Smith, 1957). Such studies are recognizably less definitive than those in which paleontological evidence is used to provide information on past distribution. In these particular groups, however, this information has not been readily available owing to the scarcity of records of the modern orders from fossil localities, and to the difficulty or impossibility of identifying those fossils that are found.

Both of these difficulties have been greatly reduced in recent years. New techniques of collecting the (usually small) fossils have been developed (*vide* Hibbard, 1949), and a revival of interest in the skeletal morphology of recent amphibians and reptiles has given some of the necessary background for the proper evaluation of their fossil record. Evaluative studies of specific characters (e.g., Johnson, 1955, 1956) are of particular pertinence in this regard.

In a recent paper on the zoogeography of the Interior Highland region (Dowling, 1958), I pointed out that the only known source of Pleistocene fossils in this region is the Conard Fissure of northwestern Arkansas. I suggested at that time that further work on the fossils of this deposit might give information on the past distribution of the herpetofauna that is not currently available. An unexpected opportunity to do some work on the fossil snakes of this locality has come

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to me through a fortunate combination of circumstances. I was awarded a fellowship at the University of Florida where Walter Auffenberg had just completed a study of the fossil snakes of that state, and, further, had borrowed the snake material from the American Museum of Natural History that Barnum Brown had collected from the Conard Fissure in 1903 and 1904. This collection, together with that obtained by us at the University of Arkansas, appears to be all the fossil snake material that is currently available from the entire Interior Highland region.

I particularly wish to thank Dr. L. E. Grinter, Dean of the Graduate School, University of Florida, for granting me time to work on this and other studies through the fellowship. I am most appreciative to Dr. Walter Auffenberg of that institution for his instruction in the identification of snake vertebrae and for a major role in the identification of the fossils reported here. I also wish to thank Dr. H. K. Wallace, Head of the Department of Biology, University of Florida, for kindly providing space and services for these studies, Dr. Edwin H. Colbert and Mrs. Rachel H. Nichols, Department of Geology and Paleontology, the American Museum of Natural History, for the use of the material in their care and for other courtesies, and Mr. S. C. Dellinger, Curator of the University of Arkansas Museum, for much aid. Abbreviations of institutions referred to in this paper are:

A.M.N.H., the American Museum of Natural History
U.A.M., the University of Arkansas Museum

PRESENT KNOWLEDGE OF THE FAUNA

The unusually rich mammalian material of the Conard Fissure was reported upon long ago by Barnum Brown (1908, p. 169), who recognized a total of 51 species, of which 24 were considered extinct. The extremely diverse material included sabre-toothed tigers as well as such ecologically differentiated recent forms as red squirrel, porcupine, and musk ox on the one hand, and peccary, spotted skunk, and horse on the other. This combination of boreal and temperate southwestern species suggests the presence of more than one faunal element in the deposit. However, this early expedition was not able to keep the material in stratigraphic sequence (*vide* Brown, 1908, p. 164), and, as most of the material at the University of Arkansas was taken from the tailings of the previous excavations, it is not yet possible to correlate any of the animals into separate faunas.

The herpetological records from the Fissure have been few. Brown (1908, pp. 166, 206–207, pl. 22) recorded *Bufo?* sp., *Rana* sp., *Rana*

?sp., lacertian sp., ophidians, and *Crotalus* sp. from his collection. The amphibians do not appear to have been studied since this original report. However, Gilmore (1928, p. 28) identified the lizard jaws as *Phrynosoma* sp. He later (1938) recognized *Coluber* cf. *C. constrictor* Linnaeus (p. 62), *Pituophis* sp. (p. 67), and confirmed Brown's previous identification of the articuloangular (A.M.N.H. No. 6404) as *Crotalus* sp. (p. 73). Brattstrom (1954, p. 37) has recently referred the *Crotalus* material to *C. horridus* Linnaeus. Thus, two (or three) anurans, a salamander, a lizard, and three genera of snakes have been reported from the Conard Fissure to this date.

SNAKES IN THE COLLECTIONS

Some 12 species of snakes representing eight genera and belonging to two families, the Colubridae and the Viperidae, are recognized in the material at hand. All have been identified from characteristics of the middorsal vertebrae, which have been shown to have relatively small amounts of intercolumnar variability by Johnson (1955) and to be useful for specific identification by Auffenberg (MS). In all cases the fossils have been compared directly with the vertebrae of the recent snakes to which the fossils are allocated, and the vertebrae of related species and genera, and of forms with similar vertebral characteristics, have been considered. Proportional measurements were utilized in the final disposition of the vertebrae where appropriate (e.g., in the genera *Elaphe*, *Lampropeltis*, and *Heterodon*).

The various forms here recognized are listed alphabetically by genus within the family.

COLUBRIDAE

CARPHOPHIS GERVAIS

Three vertebrae (U.A.M. No. 1) are indistinguishable from those of the modern species, *C. amoenus* Say. Two of these are short (anterior) vertebrae, but the one from the middorsal region shows the elongate centrum (centrum length/zygosphenic width, 1.73) that distinguishes this genus from *Sonora* Baird and Girard, and the flattened aspect of the haemal keel that effectively distinguishes it from *Diadophis* Baird and Girard.

COLUBER LINNAEUS

More than 50 per cent of the vertebrae in both collections have the elongate tapered form, narrow haemal keel, and epizygapophyseal spines that characterize this genus. As indicated by Auffenberg (MS),

while no known character will separate all the vertebrae of the species *C. constrictor* Linnaeus and those of *C. flagellum* Shaw (*vide* Auffenberg, 1955, p. 139; MS, for the use of the generic name *Coluber*), the extreme examples of both species appear to be separable on the form of the haemal keel.

In *C. constrictor* the keel tends to be flatter and its posterior end (not the anterior end, used by Brattstrom, 1955, p. 152) tends to stop more anteriorly and to have a more rounded and less distinctively separated tip than in *C. flagellum*. Thus, those vertebrae in which the haemal keel is flattened, ends well anterior to the neck of the condyle, and as a rounded ridge is hardly separated from the centrum may be allocated to *C. constrictor*. Similarly, the vertebrae in which the haemal keel is little flattened, extends over the neck of the condyle almost to its articulating surface, and ends in a sharp point that is free of the centrum may be allocated to *C. flagellum*. Even by this means somewhat less than 50 per cent of the vertebrae can be identified as to species. On these bases, however, both species have been recognized in the material (*C. constrictor*, A.M.N.H. No. 7207 [70 vertebrae], U.A.M. No. 8 [30]; *C. flagellum*, A.M.N.H. Nos. 7208–7209 [34], U.A.M. No. 9 [15]; *Coluber* sp., A.M.N.H. No. 7210 [150], U.A.M. No. 10 [56]).

ELAPHE FITZINGER

Two species of this genus have been recognized in the material. A short vertebra with high neural spine and weakly developed subcentral ridges is characteristic for the genus. Several of these vertebrae (A.M.N.H. No. 7211 [three vertebrae], U.A.M. No. 5 [two]) are referable to *E. guttata* Linnaeus on the basis of centrum length and the relative height and length of the neural spine (spine length/spine height, 1.6–1.9 at centrum lengths *ca.* 0.2 inch). However, in three other middorsal vertebrae of about the same lengths this ratio falls above 2.3. On the basis of this ratio, the rather elongate centrum, and the broad and strongly developed haemal keel, these vertebrae (A.M.N.H. No. 7212) are allocated to *E. vulpina* Baird and Girard. A number of anterior vertebrae (U.A.M. No. 6 [four]) also differ from *E. guttata* in the vertical, flattened, and square-ended shape of the hypapophysis. This shape is found in both *E. obsoleta* Say and *E. vulpina*, and the vertebrae are tentatively allocated to the latter. Several other vertebrae (A.M.N.H. No. 7213 [two], U.A.M. No. 7 [15]) have not been allocated as to species, and may be listed as *Elaphe* sp.

HETERODON LATREILLE

A number of heavy vertebrae with much depressed neural arches clearly are of this genus. They are not of *H. simus*, as shown by their length. However, the middorsal vertebrae of *H. nasicus* Baird and Girard and *H. platyrhinos* Latreille also are completely distinguishable in the recent specimens at hand, differing measurably in the over-all length of the vertebra (prezygapophysis to postzygapophysis) as compared with its width. This is not true of the specimens from the Conard Fissure, however, and pending further study they must be listed as *Heterodon* sp. (A.M.N.H. No. 7214 [four]; U.A.M. No. 11 [eight]).

LAMPROPELTIS FITZINGER

The vertebrae of this genus are short, as in *Elaphe*, but all the species appear to be separable from at least the American members of the latter genus on the bases of their lower neural spines and heavier subcentral ridges. The three species that are now found in this region are also recognized in the fossil material. Small vertebrae with the extremely short neural spines characteristic of *L. doliata* Linnaeus are the most common (A.M.N.H. No. 7215 [33], U.A.M. No. 3 [25]). Among the larger vertebrae with higher neural spines (*vide* Auffenberg, MS, for discussion), both *L. getulus* Linnaeus, with very strong subcentral ridges (U.A.M. No. 4 [four]), and *L. ?calligaster* Harlan, with less strongly developed ridges (A.M.N.H. No. 7216 [two], U.A.M. No. 2 [three]) appear to be represented.

PITUOPHIS HOLBROOK

Seven vertebrae (A.M.N.H. No. 7217) show the high neural spine and strong subcentral ridges characteristic of this genus. Five of these show the concave zygosphenic edge that is also characteristic of *Pituophis*. None shows any obvious differences from vertebrae of recent forms, and as it appears likely that all the North American snakes of this genus are conspecific (*vide* Conant, 1956, p. 29), these fossils may safely be allocated to the oldest name, *P. melanoleucus* Daudin.

THAMNOPHIS FITZINGER

This genus is represented by several vertebrae (A.M.N.H. No. 7218 [nine], U.A.M. No. 12 [three]) having the long centrum, elongate curving hypapophysis, and relatively low neural spine that is typical. All the measurable vertebrae have a neural spine higher than that found

in the *radix* group of this genus, and all are longer (centrum length/neural arch width, 1.5 or more) than those of *T. sauritus*. It seems safe, therefore, to allocate these specimens to *T. sirtalis* Linnaeus.

VIPERIDAE

Several large, heavy, and short vertebrae with long, straight, and tapering hypapophyses clearly belong to this family. Brattstrom (1954, p. 37) recently allocated some of these vertebrae along with the articuloangular (A.M.N.H. No. 6404) to *Crotalus horridus* Linnaeus. His reasons for doing so were not stated, but may have been based on geographic proximity. Other workers (Gilmore, 1938, p. 73; Auffenberg, MS) have been unable to distinguish the species of *Crotalus* on the basis of vertebral characteristics, and in many cases allocation to genus may be only tentative. The various characteristics by which Brattstrom distinguished his fossil subspecies *C. adamanteus pleistofloridanus* (1954, p. 35) from the modern form have been shown (Auffenberg, MS) to be so variable ontogenetically and intracolumnarly as to invalidate that form. Thus at present any allocation of fossil crotaline snakes to species appears highly speculative, and allocation to genus is often only slightly less so.

Among North American crotalines the presence of epizygapophyseal spines appears to be characteristic of the genus *Agkistrodon* Beauvois. Its absence is not similarly so, because vertebrae without this character are found even in this genus. However, as none of the vertebrae from the Conard Fissure possesses the epizygapophyseal spines, it appears logical to follow the previous identification of these fossils (Brown, 1908, p. 207; Gilmore, 1938, p. 73; Brattstrom, 1955, p. 37) at least to the point of ?*Crotalus* sp. These vertebrae are found in both collections (A.M.N.H. No. 7219 [49], U.A.M. No. 13 [eight]).

DISCUSSION OF FAUNA

A significant feature of the snake fauna of this deposit is the predominance of large terrestrial species of diurnal habit. Vertebrae of snakes of the genus *Coluber* are by far the most prevalent, with those of *Lampropeltis*, ?*Crotalus*, and *Elaphe* occurring in some numbers. Furthermore, no snakes of the genus *Natrix* or any other aquatic or semi-aquatic species (e.g., *Agkistrodon piscivorus*, *Thamnophis sauritus*) are found. The only natricine represented in the collection is *Thamnophis sirtalis*, a wide-ranging terrestrial species. The only snake deviating from this general picture is *Carphophis*, a burrowing species, which actually may have fallen into the pit at some more recent date.

This apparent selection of snakes suggests the activities of some kind of predator. This was also suggested by Brown (1908, p. 164) to account for the mammalian fauna. In relation to the snakes (p. 207) he stated, "Many no doubt lived there, attracted by the great number of frogs, while others were carried there by the birds." It may be pointed out, however, that none of the snakes recognized from the deposit are known to be cave inhabiting, whereas *Elaphe obsoleta*, not found here, has been reported from caves several times. The birds referred to by Brown were presumably the owls that he had suggested to account for the number and appearance of some of the smaller mammal fossils (p. 170). The completely diurnal nature of the snakes represented, plus the fact that North American owls rarely eat snakes, appear to contradict this view. Similarly, the absence of water snakes, a common prey of snake-eating hawks, seems to preclude the latter also as possible predators, as does the observation of Walter Auffenberg that snake vertebrae voided by hawks are characteristically pitted by the digestive juices. This condition was not found in any of the fossil vertebrae from the Conard Fissure, although it does appear in some Pleistocene fossils in Florida (*vide* Auffenberg). The numerous skunks and weasels found in the deposit, therefore, appear to be the most likely predators contributing to the presence of snakes there, and probably are the source of the frog bones as well.

The horned toad, *Phrynosoma*, previously identified from this deposit by Gilmore (1928, p. 28), now reaches its eastern limit more than 100 miles to the west of the Conard Fissure. Similarly, the prairie-dwelling fox snake, *Elaphe vulpina*, identified here, is now found in the glaciated areas more than 200 miles to the north. Of the other snakes found in the deposit, only *Carphophis* is a characteristic inhabitant of the eastern deciduous forest, and such typical forest inhabitants as *Cemophora coccinea*, *Elaphe obsoleta*, and *Opheodrys aestivus* are, so far at least, absent. Thus the presence of a prairie fauna in this region sometime during the Pleistocene (or during the thermal maximum shortly thereafter?) is strongly indicated by the reptiles.

Barnum Brown (1908, p. 169) had suggested habitats of "glades and forest-covered hills" to account for the mammalian faunal grouping. The snake fauna described here does not contra-indicate such an ecological situation, but certainly the "glades" are much better represented than the forests. Further information on other elements of the herpetological fauna and a reevaluation of the mammals will be necessary before a decision as to whether prairie, deciduous forest, or a mixture of faunas from both is actually demonstrated by the animals of

this deposit. The meager herpetological evidence available so far clearly points to a more arid climate than the present one.

SUMMARY

Middorsal vertebrae of snakes from the Pleistocene Conard Fissure of the Ozark Plateau are here recognized as belonging to eight genera in two families. The forms identified are: *Carphophis amoenus*, *Coluber constrictor*, *C. flagellum*, *Elaphe guttata*, *E. vulpina*, *Heterodon* sp., *Lampropeltis doliata*, *L. ?calligaster*, *L. getulus*, *Pituophis melanoleucus*, *Thamnophis sirtalis*, and *?Crotalus* sp. A predator selection of terrestrial diurnal species is suggested. The reptiles so far identified indicate a more arid climate, and perhaps typical prairie conditions, at the time of deposition. When the large number of extinct mammals previously reported from the deposit (Brown, 1908) is considered, the most surprising aspect of the snake fauna is its similarity to the present one. Only two of the recognized species are not known from the region now, and none is extinct.

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